# The Journal of HEREDITY

TWO ALBINO ALLELES IN THREE KITTENS
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Millan and George—Twins Reared Apart
The Seven Little Haploid Peppers
Juvenile Silvering in Guinea Pigs
Recessive Curly-Coat in Horses
Are War Marriages Eugenic?
Inherited Cataract in Cattle

VOLUME 34 APRIL, 1943 NUMBER 4

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*The*

# Journal of Heredity

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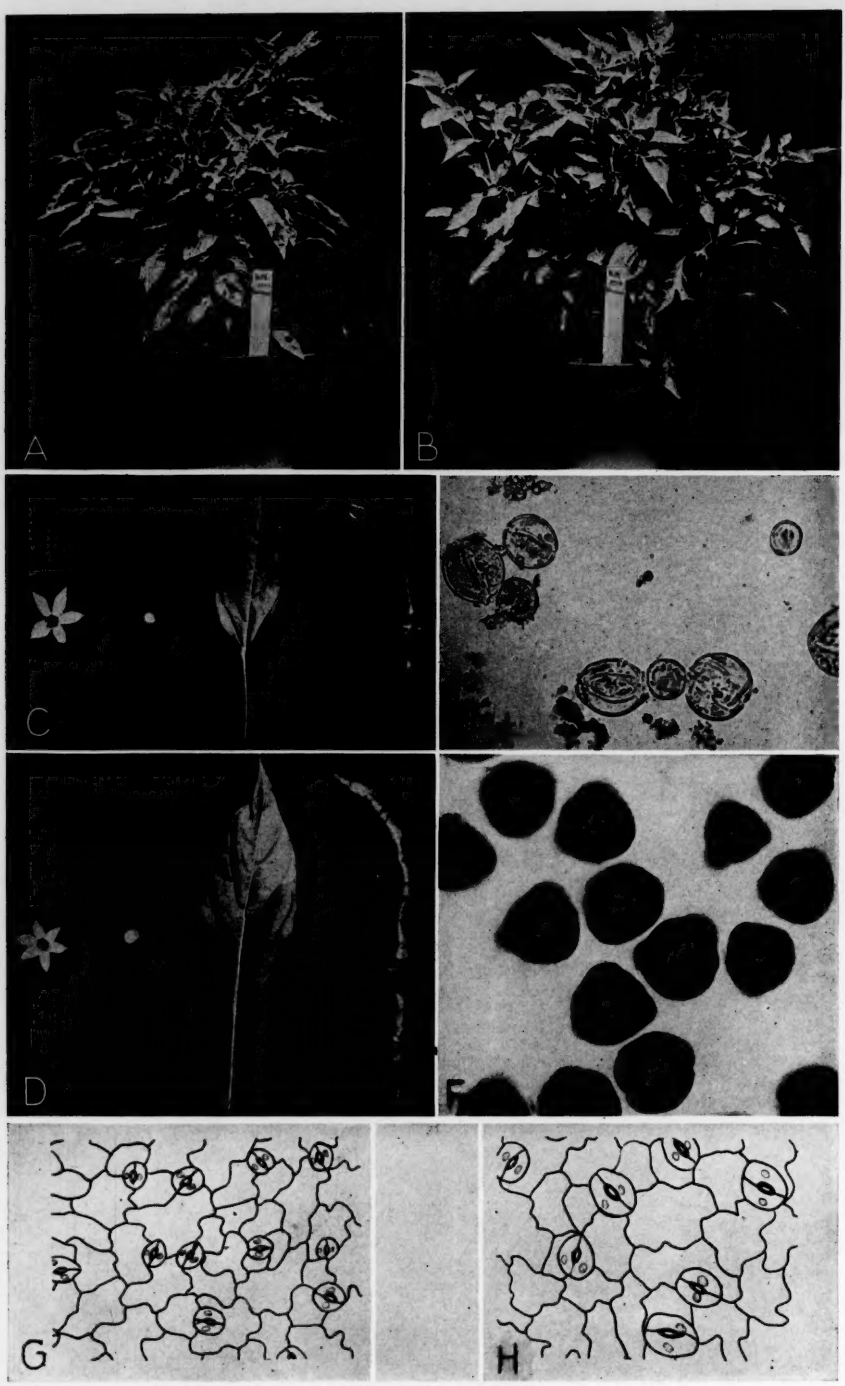



**COMPARISON OF HAPLOID AND DIPLOID PEPPERS**

**Figure 1**

*A* and *B*—Haploid and diploid plants, King of North variety, ⅛ ×; *C* and *D*—Haploid and diploid flowers, seeds and fruits, Long Red Cayenne variety, ⅔ ×; *E* and *F*—Haploid and diploid pollen, World Beater variety, 400 ×; *G* and *H*—Haploid and diploid stomata, World Beater variety, 300 ×.

# HAPLOIDS IN TWIN SEEDLINGS OF PEPPER

## Capsicum Annuum L.*

HILDE M. CHRISTENSEN AND RONALD BAMFORD

HAPLOID plants have been known to occur for a long time, dating back to 1922, when Blakeslee *et al*[2] reported the occurrence of a haploid plant in *Datura stramonium*. Since that time haploids have been observed in more than thirty genera. Darlington[5] presents an extensive list of these (p. 444), and Kostoff[10] discusses the whole haploid problem, particularly its relation to practical plant breeding.

It was not until 1933 that twin seedlings were also known to be a source of haploid plants. At that time, Kappert[7] reported the occurrence of a haploid in the twin seedlings of a species of *Linum*. Since then it has become increasingly evident that haploids are more abundant in these than they are in normal seed populations. They have been found in the twin seedlings of *Oryza*,[15] *Triticum*,[13, 14] *Gossypium*,[6, 18] *Datura*,[16] *Phleum*,[4] *Dactylis*,[18] *Poa*,[12] and many other genera.

In view of this it seemed advisable to investigate a group of twin seedlings of *Capsicum annuum* when these were made available for study in the fall of 1941. This seemed a good lead since the Solanaceae have been known to be a constant source of haploids in previous reports. The basic chromosome number of Capsicum was first reported to be six, by Kostoff[9] in 1926. However, in 1927, Vilmorin and Simonet[17] failed to confirm Kostoff's findings and reported the basic number to be twelve. Since that time their results have been substantiated by other workers, particularly Huskins and La Cour.[7]

The purpose of this work was to determine first, whether haploids were present in the twin seedlings of pepper; second, if they were present, to what extent they occurred; and third, to examine them cytologically.

### Materials and Methods

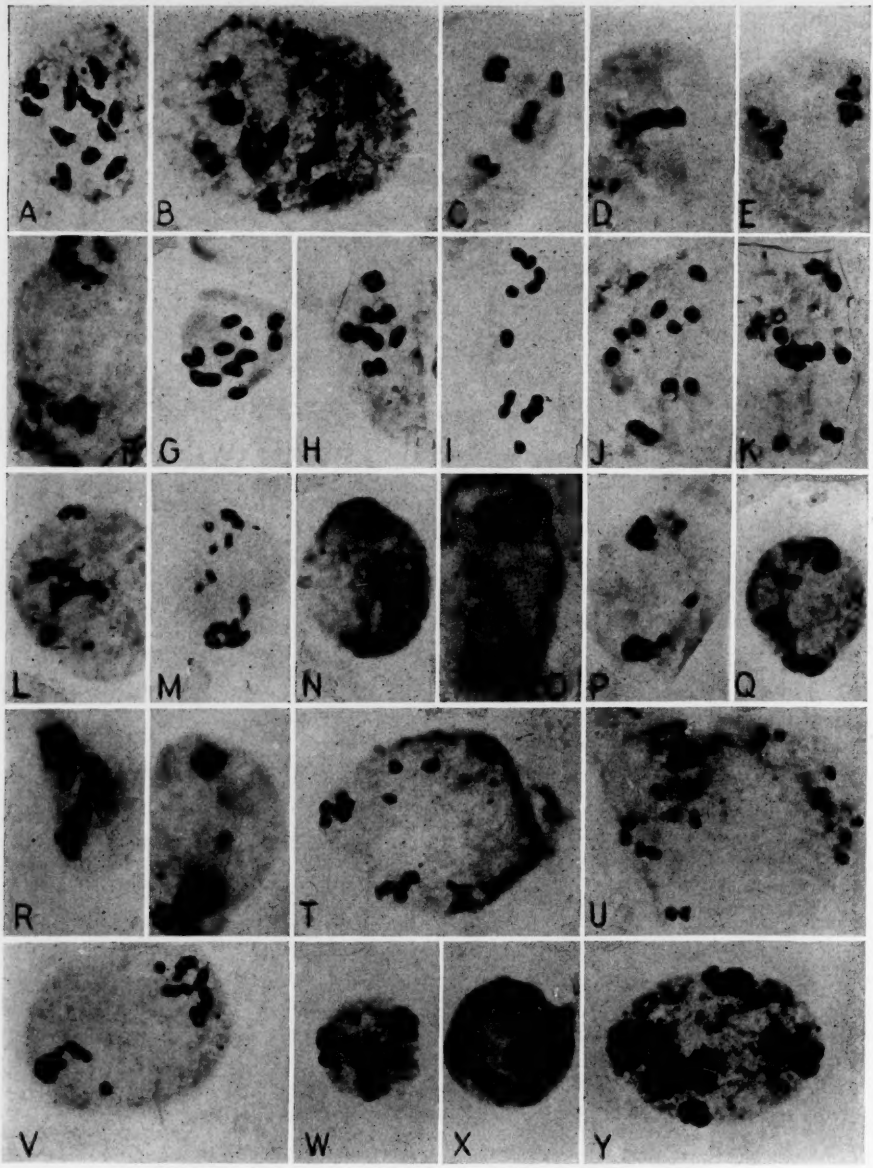
The twin seedlings used in this study were obtained from the Seed Laboratory of the Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture, Horticultural Station, Beltsville, Maryland. They were selected during germination studies which were carried on in that laboratory and were obtained through the kindness of Dr. E. H. Toole.

The total number of twin plants originally secured amounted to about two hundred pairs, representing fifteen different varieties (see Table I). Many of these plants died, so that often it was only possible to investigate one member of the original pair. The plants were numbered in the order in which they were received. Thus, number fifty was the fiftieth twin seedling. The two plants were then designated as *A* and *B*.

The plants were obtained while in the seedling stage and were grown in the greenhouse to maturity. Root tips and buds were collected and both were treated in exactly the same way, except that the root tips were first stored for twenty-four hours at a temperature of approximately 45° Fahrenheit. All material was then fixed in a 3 :1 absolute alcohol-acetic acid solution and eventually stored in 85 per cent alcohol. After this treatment, the slides were made by the regular smear technique, using propionocarmine stain. Later on, the pollen samples and epidermal mounts were made with the use of the same stain.

Chromosome counts generally were made from meiotic divisions of the pollen

*Scientific Paper No. A-37. Contribution No. 1858 of the Maryland Agricultural Experiment Station (Department of Botany).




**MEIOTIC STAGES IN HAPLOID POLLEN FORMATION**

**Figure 2**

Al the photomicrographs are meiotic stages from haploid plants except *B*. The number of the haploid (Table II) is indicated in each case. Approximately 825 ×. *A*—Haploid 110*A*, diakinesis, twelve univalents; *B*—diploid, diakinesis, twelve bivalents; *C*—108*A*, late diakinesis, chromosomes associating in pairs; *D*—108*A*, metaphase I, chromosomes associating in pairs; *E*—108*A*, anaphase I, equal separation to each pole; *F*—108*A*, telophase I, unequal separation to poles; *G*—115*B*, metaphase I, small number of chromosome associations; *H*—60*B*, metaphase I, practically all chromosomes associated with others; *I*—60*B*, anaphase I, movement to poles of associated chromosomes; *J*—36*A*, anaphase I, movement to poles of univalents; *K*—36*A*, anaphase I, note polar and middle groups; *L*—36*A*, anaphase I, division of univalents, polar groups undivided; *M*—36*A*, telophase I, lagging divided univalents; *N*—telophase I, lagging undivided univalent; *O*—60*B*, telophase I, complete division, unequal separation; *P*, *Q*—110*A*, telophase I, three and six lagging undivided univalents; *R*—60*B*, metaphase I, chains of associated chromosomes; *S*—60*B*, telophase I, rings of associated chromosomes; *T*—233*A*, anaphase II, lagging chromosomes; *U*—108*A*, anaphase II, haphazard movement of divided chromosomes; *V*—36*A*, metaphase II, note chain associations; *W*—114*B*, telophase II, lagging chromosomes; *X*—114*B*, macro- and micronuclei; *Y*—40*A*, six nuclei of like size.

mother cells; and in some cases, these determinations were confirmed by somatic counts from the root tips. The root tip material was difficult to use because of the small size of the chromosomes. Drawings were made with a camera lucida and the magnifications of these and of the photomicrographs are shown with the figures.

## Results

The results are presented in Table I and in Table II the arbitrary numbers given to the haploid plants are listed. These plants will henceforth be referred to by these numbers.

Three of these haploid plants had a normal diploid plant as their twin (40*A*, 60*B*, 114*B*) but in the case of the other haploids, the co-twin died before a chromosome count could be made. It is probable that these plants too, were the mates of normal diploids since no triploid, tetraploid or any other polyploid forms were found. The occurrence of seven haploids in the number of plants examined indicates a relatively high percentage. That this is a conservative estimate must be evident because many of the weaker plants of the twins, the most likely source of haploids, died before it was possible to examine them.

When the haploids had been identified by their chromosome number, attempts were immediately made to compare them to the diploid member of the pair or to diploids of the same variety. It was very difficult to distinguish the haploid plants by their size, flowers or leaves (Figure 1*A-D*). In general they were somewhat smaller but this could only be seen after close observation. However, when the stomata, the pollen, and later, the fruit and seed production were observed (Figure 1*C-H*) the haploid was always characterized by smaller stomata, very poor pollen, smaller fruits and rare seeds (Figure 1*E-H*). The condition of the pollen in the haploids indicates that these plants are nearly self-sterile and that the fruits and seeds produced were the result of open pollination, possibly with diploids.

Meiosis in several normal diploid types and in each haploid was observed. It was here that the haploid condition of these plants was first observed and in three cases a somatic count confirmed the meiotic one.

**TABLE II. Haploid Pepper Plants from Twin Seedlings**

| Variety | Number |
|---|---|
| World Beater | 36A, 40A |
| King of North | 233A |
| Long Red Cayenne | 60B |
| Unidentified | 108A, 110, 114B |

**TABLE I. Twin Plants of Pepper**

| Variety | Number of single twin plants | Number of pairs of twin plants | Number of Diploids | Number of Haploids |
|---|---|---|---|---|
| 1. Ruby King | 6 | 1 | 8 | 0 |
| 2. Bullnose Hot | 12 | 1 | 14 | 0 |
| 3. Early Gaint | 19 | 11 | 41 | 0 |
| 4. Neopolitan | 3 | 1 | 5 | 0 |
| 5. World Beater | 18 | 12 | 40 | 2 |
| 6. King of North | 14 | 5 | 23 | 1 |
| 7. Long Thick Cayenne | 3 | 1 | 5 | 0 |
| 8. California Wonder | 5 | 3 | 11 | 0 |
| 9. Long Red Cayenne | 0 | 1 | 1 | 1 |
| 10. Oshkosh | 4 | 1 | 6 | 0 |
| 11. Squash | 1 | 0 | 7 | 0 |
| 12. Chinese Giant | 21 | 3 | 27 | 0 |
| 13. Anaheim Chili | 1 | 0 | 1 | 0 |
| 14. Pimento | 2 | 0 | 2 | 0 |
| 15. Hungarian Wax | 5 | 0 | 5 | 0 |
| 16. Unidentified varieties | 30 | 9 | 45 | 3 |
| Total | 144 | 49 | 235 | 7 |

Total number of twins—193.

The behavior of the chromosomes during meiosis in all the haploids was very irregular when compared to corresponding diploids. In the diakinesis stage twelve univalents were often observed (Figure 2*A*) as compared to the twelve bivalents of the diploid (Figure 2*B*). However, all stages of bivalent-univalent combination could be observed and in some cases complete pairing, or at least association, was present (Figure 2*C*). Where this association was found the chromosomes formed a typical metaphase plate (Figure 2*D*) and subsequently separated (Figure 2*E*) into two groups of six chromosomes or possibly a group of five at one pole and a group of seven at the other (Figure 2*F*).

The most frequent observation was the absence of a typical metaphase plate and the presence of an irregularly arranged group of chromosomes between the two poles (Figure 2*G-K*). In these groups all types of associations were observed from 12 univalent chromosomes (Figure 2*J*) to those with some grouping of two, three or four chromosomes together (Figure 2*H-I*). In most of the haploids these various associations appeared haphazardly arranged but in one haploid (36*A*) two groups were evident. Those which were present at the poles and others which arranged themselves in between the two polar groups (Figure 2*K*). In contrast to the behavior in the other haploids, particularly 40*A* from the same variety, the central group of chromosomes divided (Figure 2*L*) and passed irregularly to the poles (Figure 2*M*). The usual behavior is for the undivided chromosomes to move the poles in a random fashion (Figure 2*P*) but generally with some lagging chromosomes left behind (Figure 2*M, O, P*). In one haploid (60*B*) the chromosomes associated in large groups (Figure 2*Q*) and eventually rings (Figure 2*R*) were formed in the following telophase.

The presence of a second meiotic division in many haploids has been questioned but it was observed in all seven *Capsicum* haploids. A repetition of the random passage of undivided chromosomes (Figure 2*S-T*), the association of chromosomes in groups and chains (Figure 2*U*), and lagging chromosomes (Figure 2*V*) which were described for the first meiotic division were in evidence. In addition to this were many observations which were impossible to analyze. The resulting telophases of the second division (Figure 2*W-X*) were always multinucleate having anywhere from four large and two small nuclei to ten nuclei of varying sizes. This irregularity undoubtedly explains the various-sized pollen grains previously mentioned (Figure 1*F*).

## Discussion

The results of these observations of the haploids of Capsicum closely agree with those which have been so excellently summarized and discussed by Kostoff[10] in a recent paper. The greater number of pairs of twins are diploids; this has been shown to be the case in *Gossypium*,[6] *Datura*[16] and other genera. It does not agree entirely with the observations of Muntzing,[12] who, in an investigation on the twin seedlings of *Triticum, Secale, Avena, Phleum, Poa Lolium* and *Solanum,* found that the greater number of the twins have the normal diploid chromosome number; but, he states" . . . when the numbers are different one of the twins is generally triploid as compared to the other one." He did find one haploid in *Phleum pratense* and one in *Solanum tuberosum.* However, in contrast to the relatively low percentage of haploids obtained by Muntzing in twin seedlings, most other workers have found high percentages of haploids in twin pairs. In cotton, Harland[6] obtained 14 sets of haploid-diploid twins from 16 pairs of seedlings. The other two sets were normal diploid-diploid pairs. This is an extremely high percentage (87.5%). Namikawa and Kawakami,[14] working with wheat, obtained one haploid-diploid set out of 29 pairs of twins. The others were: 19 diploid-diploid, eight diploid-triploid, and one diploid-tetraploid. The frequency of haploids in this case was considerably less, with a percentage of 3.4. In this work on *Capsicum* the per-

centage of haploids in twin seedlings was found to be 3.6. When these proportions of haploids from twins are compared with the ratio of occurrence of haploids from normal monoembryonic seeds, it can immediately be seen how much greater is the frequency of haploids from twin embryos as compared with haploids occurring spontaneously from single embryo seeds. To illustrate this point, Harland[6] found that the frequency of occurrence of haploids in monoembryonic seeds of Sea Island cotton varied from 0.025 to 0.05 per cent, as compared to 87.5% in twin seedlings, while Satina *et al*[16] in *Datura* found the frequency to be 0.018 per cent in an extremely large population. In the same report[16] they noted that one haploid was found among five twin seedlings. All this bears out Kostoff's general conclusion[10] that "it is probable that a great many of the spontaneously originated (rather found) haploids in nature came from haplo-diploid twins."

When the observations of meiosis in these *Capsium* haploids are compared to others (those of Belling and Blakeslee[1] to Miduno,[11] Kostoff[10] and others) they parallel such descriptions. The presence of univalent chromosomes, the random separation of these in the first meiotic division, the presence of two, three, four or more chromosomes in association with each other in chains or rings, the lack of a definite metaphase plate, and the presence of lagging chromosomes with the resultant micronuclei, have all been reported previously. This is also true of the behavior of the second meiotic division, with the eventual production of a multinucleated pollen mother cell, and the usual high proportion of shrunken and varying sized pollen grains.

The question of the possible use of haploids in a practical plant breeding program, where homozygous material is needed for genetic studies, is not settled. Boswell[3] has pointed out that in peppers there is disagreement on the inheritance of several characters. With this in mind, it would seem that the development of homozygous strains, from such haploids as those reported here, would be of help in clearing up these disagreements. However, Kostoff,[10] in discussing the potential practical breeding value of haploids, has attempted thoroughly to discredit this method as a means of securing homozygous strains. He does this chiefly on two grounds; (1) because of the difficulty of securing a number of haploids from any one variety in order that many of the genetic characters may be included in at least one; and (2) because of the apparent difficulty in doubling such haploids so that the resulting diploids will represent potential homozygous breeding material. In the case of *Capsicum* these two objections do not apply. The occurrence of two haploids (36*A* and 40*A*) from the World Beater variety, and the high percentage resulting by using only twin seedlings suggests that the first objection is not valid. In addition, the different chromosome behavior in meiotic association suggests these two haploids of World Beater are different genetically. The other objection concerning the difficulty of doubling does not apply in many of the Solanaceae since tomato, tobacco, petunia and others have repeatedly been doubled by several methods, among them: decapitation, growth substances and colchicine. It must be remembered that Kostoff's report[10] was written before our present knowledge of colchicine was so extensive, since he does not mention this procedure.

## Summary

1. Seven haploids of *Capsicum annum* have been secured.
2. These have been obtained from twin seedlings where the other member was a diploid.
3. The occurrence of these was relatively frequent compared to others from monoembryonic seeds.
4. Meiosis in the haploids is described.
5. The potential practical use of these haploids is discussed.

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## Chromosome Degeneration

Naturally self-pollinated plants show heterosis which is lost in later generations. But when hybrid corn is allowed to interpollinate, or is again inbred, not only is there a reduction in the number of normal, favorable growth genes but also there is the uncovering of the many defective loci always present in every part of the chromosome structure. The plants not only segregate within the normal complex but are rapidly reduced to the level of vigor in which the homozygous inbreds operate. Here normal heredity has a limited opportunity to find visible expression. This is proved by the fact that many of the most valuable inbred strains of corn are themselves weak and unproductive, as mentioned previously. Since they combine well with nearly all other strains they undoubtedly have good heredity but this is prevented from expressing itself because something essential is missing. All other inbreds apparently have what these good combiners lack. The fact that any part of the chromosome structure of one inbred can substitute for the homologous part from almost any other inbred shows that the mechanism must be fundamentally alike within the species. Only comparatively minor derangements keep the chromosomes from functioning at full efficiency. This renders improbable the necessity of assuming extensive differences in germinal construction. Otherwise many combinations would fail to give normal growth.

For the practical [maize] breeder the maintenance of homozygous inbred lines is a matter of serious concern. The possibility of continued production of degenerative loci must be guarded against by progeny testing or valuable lines will be lost or reduced to such a low level of vigor that they can be used only with difficulty. For theoretical genetics it is worth while to note that there is the possibility of continued degeneration. This takes place in crossbred as well as in inbred families and has nothing to do with inbreeding but is more apparent after consanguineous mating and more quickly eliminated. The prevention of chromosome degeneration and the elimination of defective loci after they are formed, in organisms not exposed to rigorous natural selection, is one of the major biological problems of the future—D. F. JONES, *Proc. Nat. Acad. Sci. Vol.* 28, p. 43. 1942.

# SILVERING IN A STRAIN OF GUINEA PIGS

ORSON N. EATON
*Bureau of Animal Industry, U. S. Department of Agriculture*

**SILVER THREADS AMONG THE BROWN**
**Figure 3**

This is an example of a complexly inherited form of silvering which reverses the usual age-sequence associated with grey hairs. These brown guinea pigs are silvered during their early months, and as they grow older the silvering disappears.

TWO different types of silvering have been described in guinea pigs. One type reported by Lambert[2] appears when the animals are three to four months old and increases as they grow older. It consists of wholly white hairs scattered in various degrees over the dorsal surface of the body. It appears on black animals and is reported to be inherited as a recessive. Another type reported by Ibsen[1] of Kansas State College, and by Wright[3] of the University of Chicago, differs from the first type in that it is most marked in the young, and becomes less distinct or entirely disappears as the animals grow older. This silvering is restricted to brown (*bb*) animals.

Microscopic examination of the silvered hairs shows a diminution of pigment except near the tip, thus making the base and mid-portions of the hair nearly or completely white. In some of the hairs there was a white band, resembling the agouti banding, just back of the pigmented tip, then pale pigmentation on to the base of the hair. On agouti hairs, this white band appeared below the agouti tip pattern, i.e., the tip of the hair was dark, next came the yellow band, then dark pigmentation again, followed by the white band or weakly pigmented portion of the hair to its base.

The character first appeared in the stock of the Bureau of Animal Industry in 1934 in a brown and red tortoise ($E^pE^pbb$) guinea pigs produced by black and red tortoise parents ($E^pE^p$

*Bb*). An example is shown in Figure 3. These traced back through several generations to four-toed stock which was brought to Beltsville by Dr. Sewall Wright in 1916, and which was originally developed by Professor W. E. Castle. Crossing with various families of the inbred strains had taken place in some of the ancestral stocks. The Castle stock had also been crossed with some of Ibsen's stock. The parents of this first silver, and two brothers and sisters of the parents, formed three matings from which all the subsequent matings producing silver descended. From these three matings and their descendants 82 matings were made (through October 31, 1942) which produced young. Of these matings 61 produced silvered young or had silvered parents. The other 21 matings were non-silvers outcrossed to other stock which failed to give silvered young in any of their progeny, and hence have not been included in the results to be presented. Two other matings, in both of which the female was an albino, have also not been included. These produced but one silver.

Eight other silvers similar to the ones above, descended from stock which also traced back to another strain obtained from Castle's laboratory and to Ibsen's stock. The mating which produced these silvers was very remotely related to the high silver-producing strain, there being nine generations back to a common ancestor. The latter case of silvering included four males and four females as well as 22 non-silvered individuals. One female was mated to a silvered male of the first silver strain and produced six non-silvered and three silvered young. These two matings have been included in the tabulations.

Several types of matings may be recognized according to the appearance of the parents and the progeny which they produced. First, classifying the progeny as to silvered and non-silvered, the following were the results:

| Parents | Progeny | | Percent |
|---|---|---|---|
| | Non-silvered | Silvered | Silvered |
| Non-silver × non-silver | 222 | 44 | 16.54 |
| Silver × non-silver | 229 | 111 | 32.65 |
| Silver × silver | 55 | 96 | 63.58 |

It will be seen at once that these figures do not represent any usual Mendelian ratio. It is also interesting to note that with one silvered parent the percentage of silvered offspring doubled that observed when neither parent was silvered; and when both parents are silvered the percentage of silvered progeny again doubled that when only one parent was silvered. The matings may be further classified as in Table I.

## Discussion

In none of these matings was silvering observed on an animal which was not brown. In one of the discarded matings in which the female was an albino, two young were recorded as medium sepia ruby-eyed ($c^rc^a$). They were also recorded as being silvered, the silvering being around one shoulder on one animal and on various portions of the dorsal surface of the other. The classification of these two animals is questionable, however. According to the appearance of the sire, of the dam and of young which were produced, the sire must have been $c^rc^a$ *Bb* and the dam $c^ac^a$ *Bb*. Therefore the two young in question could have been ruby-eyed browns and the white marked in the records as silvered could represent the tortoise factor ($E^p$), but white because of the $c^rc^a$ dilution factors. Other young were produced by this mating which were unquestionably $E^pE^pc^rc^a$. The fact that silvering appears only on browns suggests the possibility of linkage with *b*, but if this were the case, all browns should be silvered unless crossingover occurs. If crossovers take place, silvered blacks should appear occasionally. Silvering must be transmitted, however, by animals heterzygous for brown (*Bb*), as 48 out of the 251 silvers produced had one or both parents *Bb*.

Ibsen[1] suggested that silvering was due to a semidominant factor. However, its heredity does not fulfill the requirements for either a dominant or a recessive. If it were dominant a larger percentage of silvers should result from silvered × non-silvered matings than were observed, and there should be no

silvers from non-silver × non-silver. On the other hand, if it were recessive, only silver should be produced from silver × silver matings.

The data agree with that of Wright[3] and of Ibsen[1] in that only intense (*C*—) animals show silvering.

Silvering was present on self (*E*) and on tortoise ($E^p$) animals and on agoutis (*A*) and non-agoutis (*a*). The silvering was stronger on the agoutis, however.

Silvering has not been observed on homozygous piebalds (*ss*), but was present on some showing a very small amount of white, as a white toe or a few white hairs on the nose or between the ears, probably with the formula *Ss*.

The degree of silvering varied from a few silvered hairs on the nose and face to strong silvering over the whole dorsal surface of the animal. Classification of the degree of silvering into slight, medium and full gave 185, 35 and 31 for each class respectively. There seems to be no correlation between the amount of silvering on parents and on offspring according to this classification.

Sex of the silvered animals was nearly equally divided there being 123 males and 128 females.

In view of the fact that our stocks are related to Wright's and to Ibsen's, it seems probable that the silvering is from a common source, namely, the Ibsen stock. Apparently the silvering is not a recent mutation, but probably has been carried for several years in the stock of the three laboratories concerned. Its relatively recent appearance probably resulted from a shuffling of several genes until the proper combination occurred to produce visible silvering.

## Summary

A silvering factor is reported for the guinea pig which is visible at birth and gradually disappears as the animal reaches maturity. It is restricted to brown animals carrying the intensity factor *C*, but appears on agoutis and non-agoutis, and on self and tortoise animals. It has not been observed on homozygous piebalds (*ss*). Its inheritance is complex. Since the stock in three laboratories in which silvering has appeared is related, it seems probable that the silvering had a common source of origin.

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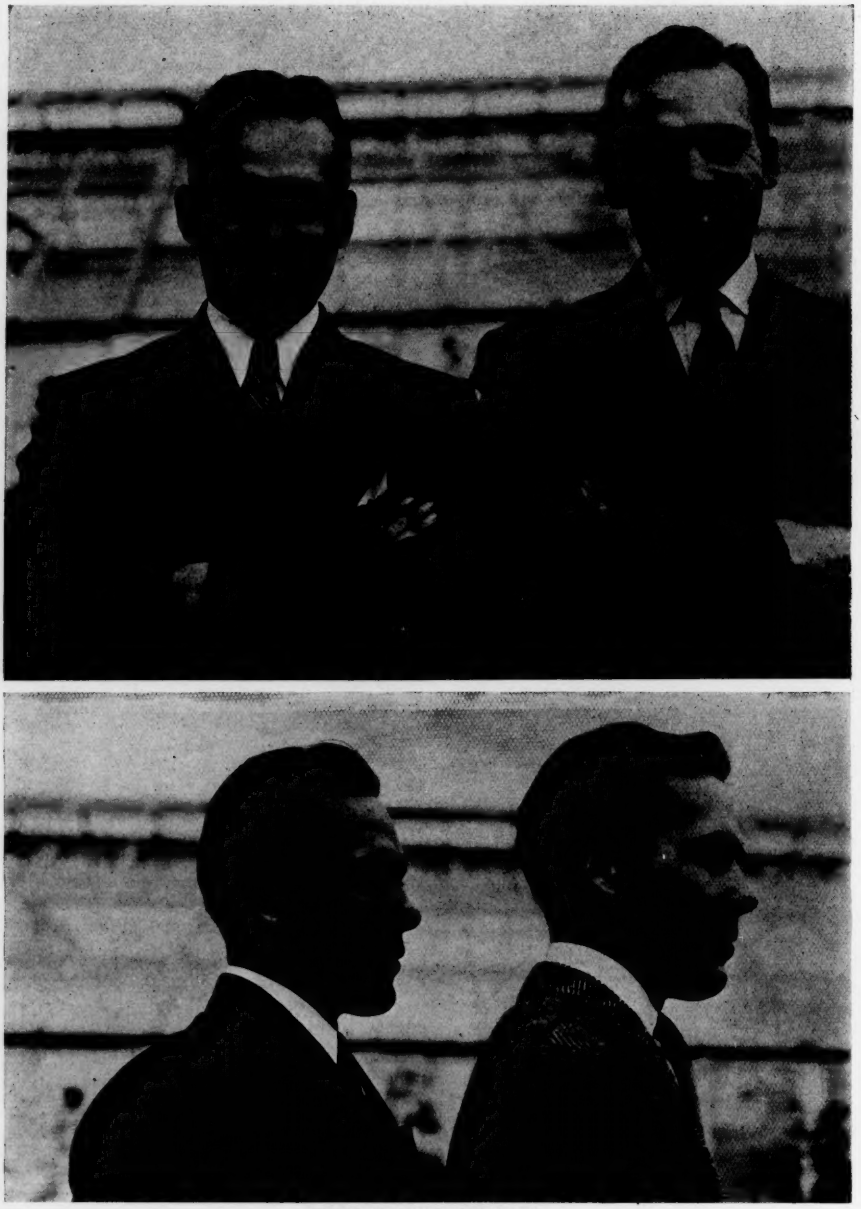
Table I. – Silvering and sex distribution in various types of guinea pig matings. B represents non-brown animals, b browns, and Bb heterozygotes.

| | Type of Mating | | | No. of matings | Non-silver B | Non-silver b | Silver b | Total classified | Undetermined * | Non-silver Males | Non-silver Females | Silver Males | Silver Females |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Bb | x | Bb | 10 | 121 | 29 | 30 | 180 | 16 | 83 | 67 | 13 | 17 |
| 2 | Bb | x | bb | 2 | 18 | 12 | 2 | 32 | 6 | 11 | 19 | 2 | |
| 3 | bb | x | bb | 5 | | 42 | 12 | 54 | 6 | 18 | 24 | 6 | 6 |
| 4 | bb(silver)x | | BB | 4 | 38 | | | 38 | 5 | 21 | 17 | | |
| 5 | bb(silver)x | | Bb | 7 | 52 | 36 | 16 | 104 | | 43 | 45 | 8 | 8 |
| 6 | bb(silver)x | | bb | 18 | | 103 | 95 | 198 | 6 | 62 | 41 | 47 | 48 |
| 7 | bb(silver)x | bb | (silver) | 14 | | 55 | 96 | 151 | 3 | 32 | 23 | 47 | 49 |
| | | | | 60 | 229 | 277 | 251 | 757 | 42 | 270 | 236 | 123 | 128 |

* This group includes albinos and reds on which silvering can not be determined.



**GEORGE AND MILLAN**

**Figure 4**

George (left) and Millan were separated immediately after birth and grew up not knowing they were twins. George has spent most of his life in New York City, while Millan has grown up where he was born, in Salt Lake City. In spite of differences of schooling and environment the boys look strikingly alike, and resemble each other closely in mental tests.

# THE CASE OF MILLAN AND GEORGE

## Identical Twins, Reared Apart

F. E. Stephens and R. B. Thompson

IN attempting to evaluate the relative effects of heredity and environment in determining human characteristics, one is constantly confronted with the difficulty of holding either heredity or environment constant while the other factor is varied. For this reason identical twins reared apart have a special interest since the heredity is identical (barring mutation) while the environment may be very different. Twenty cases have been reported by Newman[3] and his associates[4] and one by Popenoe[5] and by Muller.[2] Since such cases occur only very infrequently, it is of the utmost importance that every one of them be recorded. The following account of separated identical twins is submitted in the hope that it may be a useful addition to these slowly accumulating data.

Classification of the environment presents a difficult problem in evaluating such cases. What kind of environment and how great a change in this environment is necessary to produce significant differences in two genetically identical individuals, is a matter about which too little is known. An environmental differential which might be sufficient to produce a significant change in one of a paired set of identical genotypes might not be effective in producing a comparable change in a second genotype. The study and evaluation of greater numbers of identical twins reared apart undoubtedly will throw much light on this important problem.

### History

The twins George and Millan were born in Salt Lake City to a young couple who had previously had one child. Due to adverse family conditions their parents were unable to care for the twins. Immediately after birth they were separated and adopted into different families.

Millan was taken by a childless young couple in Salt Lake City, who later adopted a daughter. He was reared in a good environment, completed four years of high school, but did not care to go to college. His foster parents had high school training, are active church workers, and are good substantial citizens. The foster father is purchasing agent for a large commercial concern.

George was adopted by a newspaper man and his wife, also of Salt Lake City. They had no other children nor did they adopt any more. When he was about three years of age, the family moved to Colorado where they lived for three or four years. They next moved to Chicago for a few months, then to New York City, where George lived as an only child of the family, unaware that he was adopted. He had very little high school education and did not seem to be interested in school. He did become interested in commercial art, however, and followed it as a business. His foster father had a high school education and is now a make-up man on a newspaper. His foster mother had little formal education. The financial status of the two families is approximately the same.

When George was eighteen years of age, his foster parents informed him that he was adopted, and told him that he had relatives living in Salt Lake City. Just prior to this time Millan had discovered his true family relationship and talked of going to New York to find George. The following summer George came to Salt Lake City. His mother was dead, but he met his twin brother Millan, his older brother, and his real father. George's foster aunt was a former genetics student at the University of Utah. She introduced the twins to the writers of this article and the boys agreed to cooperate in a study of their similarities and differences. They are splendid young men and each seemed thoroughly to enjoy the novel experience of getting acquainted with a twin brother whose exis-

tence had just recently been revealed. They were very cooperative and took delight in discussing their similarities and differences. The twins were 19 years old when this study was made. It consists of a number of general comparisons and mental tests, comparisons of physical examinations, certain anthropological measurements, finger prints, palm prints, and tests for taste deficiency and blood groups.

The physical examinations were made by the Physical Education Department of the University of Utah under the direction of Dr. H. L. Marshall, head of the Department.

## Results of Physical Examination

### *General Appearance*

*George:* The general appearance is robust and athletic. He is an excellent example of young manhood, of fine muscular development and well tanned by exposure to the sun. Nothing unusual was discovered in the chest, lungs, or heart.

*Millan:* The general appearance is muscular and robust although the muscular development is a little less athletic and the skin is considerably less tanned than George's. The chest, heart and lungs were essentially normal.

### *Finger and Palm Prints*

Finger and palm prints of the two boys were taken* and submitted with other data to Dr. H. H. Newman. After checking over the material, Dr. Newman diagnosed the twins as monozygotic. In regard to the finger prints he stated: "With the exception of thumb prints, the digit prints are strikingly similar. George's thumb prints are both arches while Millan's are both large ulnar loops, but such differences as this are not infrequent in one-egg twins. Because of this one difference in finger prints, the ridge counts are pretty far apart, but those of the four fingers are extremely close, with George having a total of 130 and Millan, 128." In the palm prints, cross resemblances are a little greater than are the two hands of the same individual. The formulae for the finger and palm prints are given below.†

## General Information

The photographs give a fair representation of the resemblance of the two boys. When George visited in Salt Lake City, neighbors of Millan mistook him for his brother. The differences in size might have been influenced by the locality in which they were reared. It is interesting that the "city boy" is definitely the more rugged physically. The differences in head shape could have been produced if George had been permitted to lie on the back of his head when a baby. Their hair is identical in color and texture, and the hair lines are the same. The eye colors are identical and so far as could be detected by general observation have the same pigment pattern on the iris. George's skin was much

*The finger and palm prints of Millan and George are deposited in the American Documentation Service. They may be obtained from the nonprofit Bibliofilm Service, 1719 N St., N. W., Washington, D. C., by ordering Document 1657, remitting 25 cents for copy in microfilm, readably enlarged full-size on reading machine or hand viewer, or 40 cents for copy in the form of paper photoprints readable without optical aid. Since the resemblances are great enough to be very strong evidence of monozygosity, it is believed that this method of making the prints available to other workers is adequate in the interests of economy and conservation.

†***Finger Patterns***

| | *Left* | *Right* |
|---|---|---|
| George | A. $W^{lr}$. W. W. $W^{lu}$. | A. $W^{lr}$. U. W. $W^{lu}$. |
| Millan | U. $W^{lr}$. W. W. $W^{lu}$. | U. W. $W^{u}$. W. $W^{lu}$. |

***Palm Patterns***

| | *Left* | *Right* |
|---|---|---|
| George | x. 5″. 5″. 4 - ? - $A^{u}$. O. O. V. O. | 11. x. 7. H - t′ - $L^{r}$. O. O. V. O. |
| Millan | 11(10). x. 7(6). 4 - ? - $A^{u}$. O. O. V. O. | 11. 9. 7. 5′ - ? - $A^{u}$. O. O. L. O. |

tanned because of his working in the sun. Millan worked inside and showed very little tan. Their teeth are very much the same as is shown by the report of the physical examination. In almost all cases where a cavity was noted in a tooth of one boy, the corresponding tooth of the other was also affected. Their hands and fingers are very similar in appearance. Both boys belong to the "O" blood group and react positively to the phenyl thio carbamide taste test.

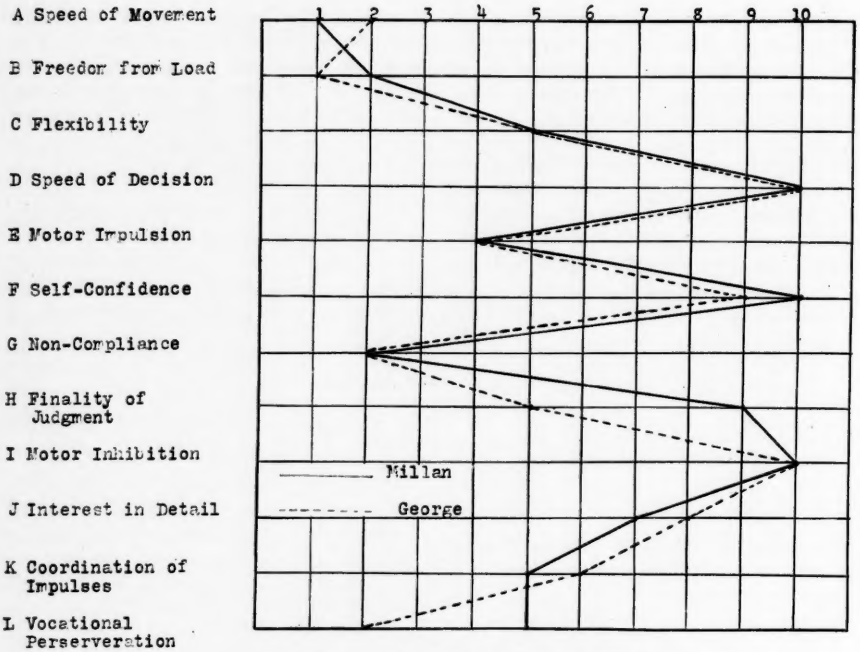
George is left handed, while Millan is right handed. Millan stated, however, that he was originally left handed, but when a youngster learned to use his right hand because of an injury to his left. The hair whorl of each is clockwise and a little back of center.

### Mental Tests

The following mental tests were made by Dr. R. B. Thompson: Progressive Achievement Tests, the Chapman-Cook Speed of Reading Test, the Otis Self-Administering Test of Mental Ability,

***Physical Tests and Measurements***

| | George | Millan |
|---|---|---|
| *Vision:* | Right: 20/100<br>Left: 20/100 | Right: 20/100<br>Left: 20/50 |
| *Color Vision:* | Normal | Normal |
| *Eyes:* | Grayish blue<br>Normal reaction to light and accommodation | Grayish blue<br>Normal reaction to light and accommodation |
| *Hearing:* | Normal | Normal |
| *Nares:* | Slight deviation of septum to left | Essentially normal |
| *Teeth:* | Well grown, in excellent condition and identical in appearance with those of Millan. The one cusp of the left upper 3rd molar tooth is just protruding. The other 3rd molars are not visible. | Well grown and in good condition and apparently identical in appearance with those of George. One cusp of the right upper 3rd molar was protruding through gums. Other 3rd molars are not visible. |
| *Height:* | 65¼ inches | 66½ inches |
| *Weight:* | 133 lbs. | 135½ lbs. |
| *Breadth of iliac crests:* | 26.4 cm. | 27 cm. |
| *Average weight for age pelvic width:* | 125 lbs. | 133 lbs. |
| *Chest Circumference:* | Inhalation: 34¾ in.<br>Exhalation: 32¼ in. | Inhalation: 36 in.<br>Exhalation: 33½ in. |
| *Pulse Rate:* | Standing: 92<br>After Exercise: 100<br>Heart returned to rest rate ½ minute after exercise. | Standing: 100<br>After Exercise: 116<br>Heart returned to rest rate ½ minute after exercise. |
| *Blood Pressure:* | Systolic: 138<br>Diastolic: 86 | Systolic: 134<br>Diastolic: 92 |
| *Urinalysis:* | Albumin: none<br>Sugar: none | Albumin: none<br>Sugar: none |




**DOWNEY WILL-TEMPERAMENT TEST**

**Figure 5**

This test is supposed to measure inherent characteristics. The remarkable resemblances in the score of these two separated twins indicates that this is so.

the Henmon-Nelson Test of Mental Ability, the Downey-Group Will-Temperament Test and the California Test of Personality.

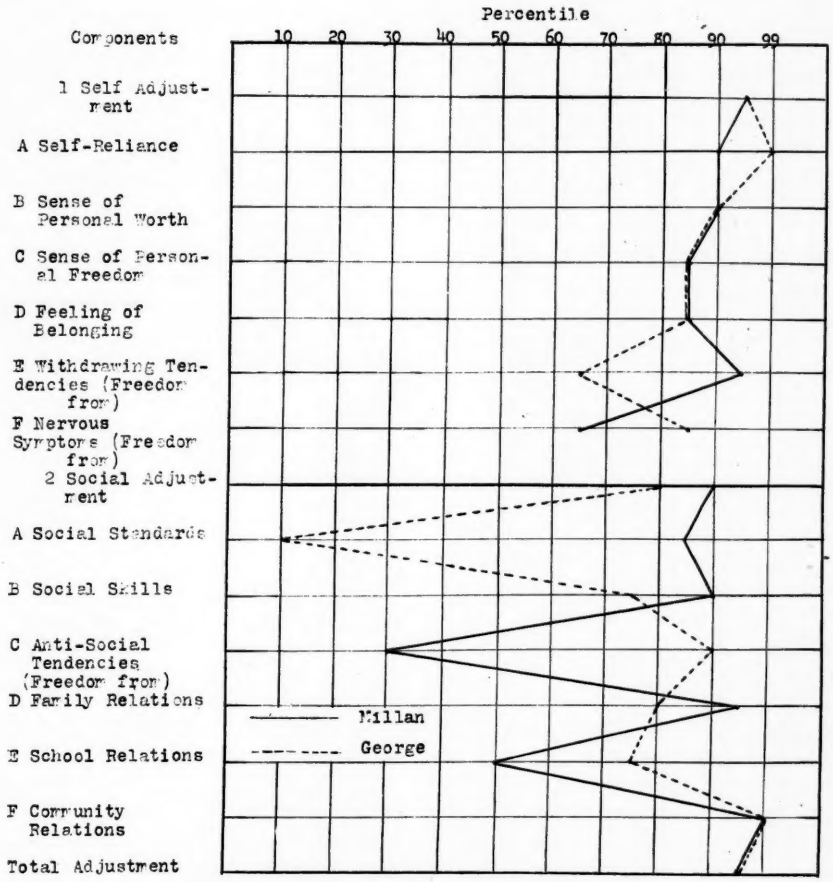
***Tests of Ability***

The two boys were given parts of the Progressive-Achievement Test, Advanced Battery, Form "A". As might

***Anthropological Measurements***

Anthropological measurements were made by Professor Elmer Smith, Anthropologist at the University of Utah.

| | George | Millan |
|---|---|---|
| *Head:* | Length: 180.4 mm.<br>Width: 150.2 mm. | Length: 190.5 mm.<br>Width: 140.6 mm. |
| *Cephalic Index:* | 83+ | 73+ |
| *Nose:* | Length: 52.5 mm.<br>Width: 32.5 mm. | Length: 53.0 mm.<br>Width: 34.0 mm. |
| *Facial Length:* (*Prosthion Nasion*) | 125.1 mm. | 125.1 mm. |
| *Hand Length:* | Right: 170 mm.<br>Left: 171.5 mm. | Right: 172.5 mm.<br>Left: 172.5 mm. |




**THE CALIFORNIA TEST OF PERSONALITY**

**Figure 6**

The marked differences in some of these test items may reflect the different environment of the two boys.

be expected, Millan ranked slightly higher than George in all parts of the test, since Millan had the opportunity of completing his high school training and George had very little high school credit. Because of the lack of time, the entire test was not given.

The Chapman-Cook Speed of Reading Test, Form "A" was given to both boys. Millan received a score of 14, while George received a score of 12. This gives Millan a ranking of medium-low for grade 8, and George a ranking of low.

***Tests of Mental Ability***

The Otis Self-Administering Test of Mental Ability, Higher Examination, Form "A", was given and Millan showed an I.Q. of 104, while George showed an I.Q. of 97.

The Henmon-Nelson Test of Mental Ability, Grades 7 to 12, was given to both boys. On this test, Millan showed an I.Q. of 101, while George showed an I.Q. of 98. The similarities were even more striking than the nearly identical I.Q.'s. When the questions which were missed by both boys in these two tests

were compared it was found both twins had missed the same questions in many cases. Each boy showed a weakness in mathematics and word meanings. It would seem after careful examination of both of these mental tests that the boys were very similar in ability and specific mental traits as far as it was possible to measure them.

### *Tests of Personality*

The Downey-Group Will-Temperament Test and the California Test of Personality, Secondary Form "A", were given to both boys.

The Downey-Group Will-Temperament Test is assumed to measure inherited characteristics, while the California Test of Personality attempts to measure many traits which are believed to be acquired by a variation in environments.

In the California Test of Personality, the first part of the test concerns self-adjustment. In this phase of the test the two boys were very similar in their attitudes. The second part of the test deals with social adjustment. In this part of the test the difference in their home, school, and community environment is shown very plainly. The greatest variation is in social standards, freedom from anti-social tendencies, and school relations. In spite of these wide variations the boys made only 20 responses which differed in the 180 questions asked.

The results of the Downey-Group Will-Temperament Test were extremely similar. When it was noted that these test results were almost identical, the complete tests were rechecked again, and after careful examination of the specific responses, the marked similarity of response was confirmed.

## General Conclusions

The evidence available indicates that George and Millan are monozygotic twins. They differ somewhat in certain physical characteristics such as size and head shape, but are remarkably alike in other physical characteristics. There is a slight difference in certain social attitudes, but there is very little difference in their mental tests and general mental characteristics.

In many respects they are similar to Newman's twins, Harold and Holden. Both pairs were adopted at birth and both were tested at the age of nineteen years. In the Otis Intelligence Test there was five points difference between Harold and Holden and four points difference between George and Millan. They were also very similar in the Downey Will-Temperament Test. From the graph (Figure 5) it will be seen that George and Millan are remarkably alike, being identical in five of the twelve points measured and with a difference of only one point in five other items.

George appears to be a little more sophisticated than Millan. Millan is interested in music while George likes drawing. Both like sports and are particularly interested in boxing. They have both boxed in public matches and have received championships in their respective classes. Their environments were decidedly different. George was brought up in a large eastern city as an only child while Millan was reared in a western city with an adopted sister. There seemed to be little resemblance in the general home attitudes and interests of the two families. But these differences in environment were not sufficient to bring about any great variance in the characteristics studied. It appears that the influence of heredity has been very great in shaping the lives of these two boys.

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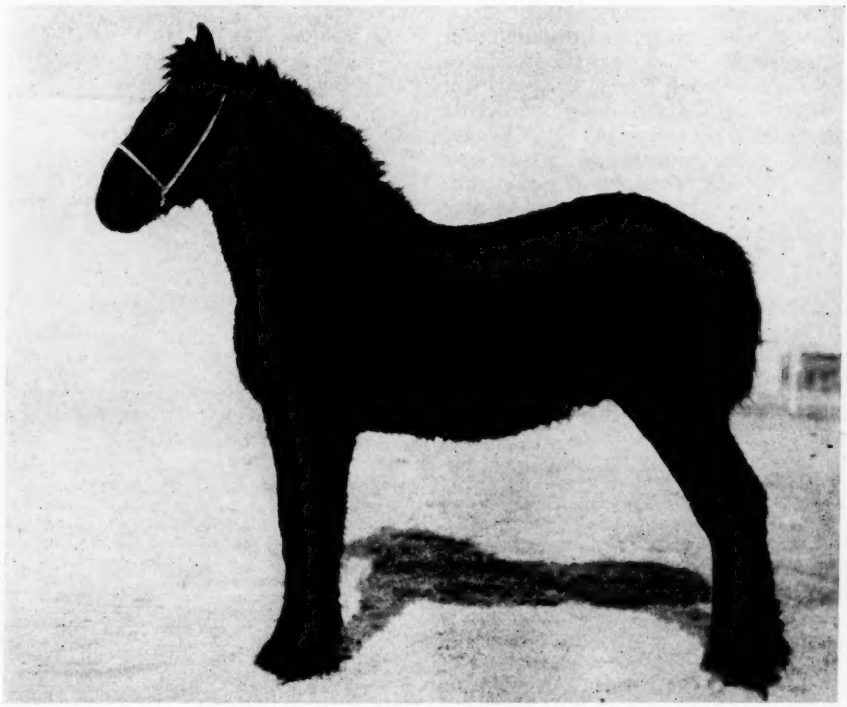
# CURLY COAT OF HORSES*

LEONARD H. BLAKESLEE, R. S. HUDSON AND H. R. HUNT†



**YEARLING CURLY-COAT**

**Figure 7**

Sixteen related Percheron mares have produced 42 colts, of which five have had curly coats. A study of the relationship of these mares and of the gene-frequency expectations indicates that a recessive gene is responsible for this variation. The colt shown here is Colonel Laet 207619, whose pedigree is given in Figure 9.

THE occurrence of curly hair coat in domestic animals is very uncommon. This condition, however, is of economic importance especially in purebred animals, since it is abnormal and may detract from their value as breeders.

Rhoads[3] reported a condition called "woolly hair" in swine which according to his description appears similar to the curly coat of horses. He states that: "six matings consisting of four outcrosses, one back-cross and one brother-sister mating indicate that woolly hair condition in swine is due to a single mendelian factor completely dominant over

*Journal article number 483 new series of the Michigan Agricultural Experiment Station, East Lansing, Michigan. Data for this paper were taken from a thesis submitted by the senior author to the Graduate School of Michigan State College.

†Research Assistant in Animal Husbandry, Research Associate in Animal Husbandry, and Professor of Zoology respectively.

normal straight hair, the recessive condition."

Cole[1] reported a defective condition of hair and teeth in a herd of Wisconsin, Holstein-Friesian cattle. He suggests that this defect might be attributed to a genetic cause rather than to factors of the environment or to faulty nutrition.

Craft and Blizzard[2] describe in cattle a semi-hairless condition which is also curly in appearance. These workers state: "Experimental matings substantiate the suggestion that the semi-hairless condition is a hereditary recessive character."

Recently the work of Shchekin and Kalaev[4] has come to the attention of the authors. The abstract which follows is in line with the author's conclusions:

> It was observed that curly coat is frequently met with in Lokai horses, among which its incidence is estimated at about three per cent. Experiments were made in a stud of Lokais at Stalinabad during 1934-37. Matings of curly animals gave 46 curly : 13 normal, and of curly × normal, 17 curly : 20 normal. It may be concluded that curliness is caused by a single recessive gene. There is no sex-linkage and coat color plays no part. About 1/3 of curly offspring from matings of curly parents show a more marked degree of curliness at birth, and it is thought that these may be homozygotes. The difference disappears later.

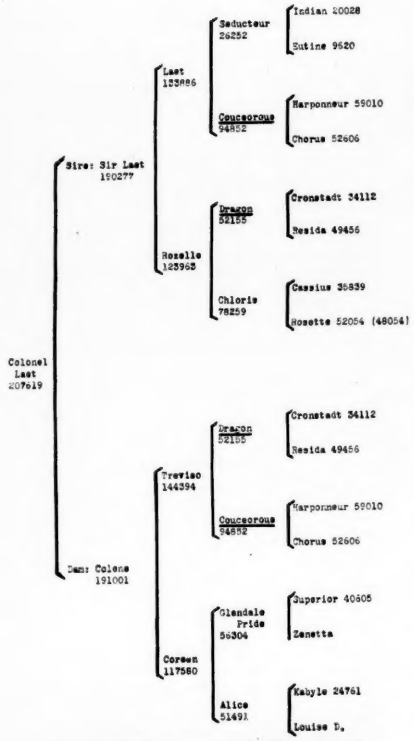
## Occurrence of Curly Coat in Horses

On March 27, 1931, a colt was foaled by a grey Percheron mare, Colene 191001, owned by the Michigan State College. This foal was sired by Sir Laet 190277, but did not live. The foal seemed normal in all respects, but possessed a very curly type of hair coat over the entire body. Little attention was given to this peculiar condition, except to note the peculiarity in the foaling records. The following year on April 7, 1932, Colene again foaled another colt sired by Sir Laet; this also had curly hair. This colt (Figure 7) developed into a good stallion, and was registered as Colonel Laet 207619. He was sold in 1933 to a purebred Percheron breeder who still has him in use as a herd sire. As far as the writers can determine, no curly foals have been sired by this stallion. Two days after Colonel Laet was foaled, a curly-coated filly was foaled by Queen Eagle 202035. This filly, later registered as Queenet 208683, was also sired by Sir Laet. Exactly a year later, on April 9, 1933, a full-sister of Colene's, Coro 197515, foaled a colt with a curly coat. Again the sire was Sir Laet. The animals whose mating produced these curly-coated young were related through several ancestors as shown in the accompanying pedigree. All of the dams who produced curly foals were sired by Treviso 144394 (a half-brother of Sir Laet's sire), or were of Treviso breeding. The interrelations of these pedigrees strongly suggested that curly coat is a recessive brought out by inbreeding.

Since 1933, four other curly foals, one male and three females, have appeared. All are of the same ancestry as the first four. In the curly animals numbered 6 and 7, we find a slight difference in the parentage. No. 6 is out of a mare whose dam was by Treviso, though the sire is Sir Laet. Curly filly No. 7 is sired by

**COLONEL LAET AS A FOAL**
**Figure 8**

The curly coat can be readily identified shortly after birth and persists apparently through life.




**PEDIGREE OF COLONEL LAET**
**Figure 9**

There is inbreeding to two ancestors, Couceorous and Dragon. Since Dragon's daughter, Roselle, had a slightly curly coat, it is probable that the gene is transmitted through him rather than through Couceorous.

a son of Sir Laet and out of a granddaughter of Treviso. No. 8 filly is out of a daughter of Treviso and by a son of Sir Laet. The ancestry of these animals and the fact that no other curly-coated individuals are known, gives further proof that the Sir Laet × Treviso cross is responsible for the appearance of this genetic anomaly. If we accept this as true, then from what common ancestor and in what manner is this curly coat inherited?

In an effort to answer the foregoing questions, the writers obtained data on all available mares which were sired by Treviso or by sons of Teviso and bred back to Sir Laet. This survey, when summarized, involved 28 mares. Sixteen of these daughters of Treviso had 42 foals whose sire was Sir Laet. (Table I.) Of these 42 foals, 5 were curly-coated and 37 smooth-coated. Assuming that Treviso is heterozygous for the recessive curly factor, then 50 per cent of his daughters would be heterozygous for the same factor; and the other half would be homozygous for smooth hair coat. Mating Sir Laet, also heterozygous for curly, to these daughters of Treviso should result in one-eighth of the 42 offspring being homozygous curly, one-half heterozygous curly, and three-eighths, homozygous smooth haired. On this basis, the expected ratio would be 36.75 smooth-coated foals and 5.25 curly-coated foals. The actual ratio was 37 to 5 or the closest possible approach to the numbers expected to make a perfect ratio.

An examination of all pedigrees, all of which are similar to that of Colonel Laet 207619 (Figure 9), reveals that

**TABLE I. Curly and Smooth Foals of Similar Breeding**

| *Mares by Treviso* | *Foals by Sir Laet* |
|---|---|
| Colene 191001 | *2 curly males* #1 & #2‡<br>3 normal foals, (2 males, 1 female) |
| Cole 194276 | 3 normal males |
| Coro 197515 | 3 normal males<br>*1 curly male, #4* |
| Treva 203692 | 1 normal female<br>1 normal male |
| Maroline 196806 | 4 normal females |
| Claudette 222940* | *1 curly female, #6* |
| Marge 216012 | *1 curly male, #5* |
| Clauro 191003 | *1 curly female, #8*† |
| Allia 196831 | 2 normal foals |
| Maroline 196806 | 4 normal males |
| Fashion 182195 | 2 normal foals |
| Ota 199928 | 1 normal foal |
| Doritea 199930 | 1 normal male<br>2 normal females |
| Lady Koncarcleviso 213435 | *1 curly female, #7* |
| Trevaret 195875 | 1 normal male |
| Leina 200584 | 4 normal foals |
| Leola 191002 | 4 normal females<br>1 normal male |
| Queen Eagle 202035 | *1 curly female, #3* |

*These mares are of Treviso breeding, but not by Treviso.
†These foals are by a son of Sir Laet.
‡Reference numbers.

there are two common ancestors in the pedigree of Sir Laet and Treviso. One is Dragon 52155, who was the sire of Treviso and also the sire of Sir Laet's dam, Rozelle 123963. The other is Couceorous 94852, who was the dam of Treviso and also the dam of Sir Laet's sire, Laet 133886. Correspondence with caretakers and owners of these individuals revealed that Rozelle, the dam of Sir Laet, possessed a slightly curly coat. Her fore-top, mane and tail were always especially curly. This information convinces the writers that the curly coat factor is inherited through the common ancestor Dragon. Couceorous, the other common ancestor, apparently is not a carrier of the curly factor since her son, Laet, was mated five or more times to Rozelle. All of the foals have had straight hair, as far as the writer can determine.

**Summary**

In this study 16 purebred Percheron mares sired by Treviso 144394 and bred to Sir Laet 190277 bore 42 foals, of whom five possessed curly coats.

This curly coated condition, according to present information, is inherited as a mendelian recessive.

The common ancestor who apparently carried the curly coat gene was Dragon 52155, the sire of Treviso 144394 and grandsire of Sir Laet 190277.

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## The Immortal Paramecium

An animal that has produced 21,000 generations of offspring and yet is still alive is celebrating its 35th anniversary in the Osborn Zoological Laboratory of Yale University.

The animal in question is of a race of the microscopic water-dweller known as paramecium or slipper-animalcule. Because this particular race was started on its career of biological immortality by Prof. Lorande Loss Woodruff, it has come to be known as the Woodruff race.

Paramecium is able to reproduce itself indefinitely by simply dividing in two, without any sex process. Each of the two parts rapidly grows again to original size, so that each can claim to be the original individual; also, barring accidents, this continuously dividing-and-multiplying individual never dies. So that we arrive at the paradoxical situation of having millions of microscopic animals, each with as good a claim as any of the others of being the founder of the line, and all of them 21,000 generations old without having experienced death.

Of course, the great majority of the offspring of the Woodruff paramecium race have been discarded and destroyed. If all had been kept, and food enough could have been provided, the race would in the first five years have packed all known space, out to the farthest stars, with a solid mass of paramecia.

This race of microörganisms has passed through 21,000 of its generations in little more than the time reckoned as one human generation. In human terms, 21,000 generations would be 630,000 years—a period going back to the haziest conjectural beginnings of the most primitive prehistoric human beings.—*Science News Letter.*

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## Capital Investment

Improvements in heredity are permanent and each generation stands on the shoulders of the preceding one, whereas improvements in the environment produce almost their full effect on the animals for which they are first made. Each new generation must again receive the improved environment or the gain will be lost. Hence, in the long run it may be profitable to spend considerable effort to make small improvements in heredity, since the expense of making such improvements in one generation may yield in dividends for many generations. The expense of making improvements in heredity (so far as those are additive) is a capital investment; the expense of making improvements in environment is an operating expense. Naturally the breeder will wish to do both so far as they are profitable.—Lush, J. L. *Animal Breeding Plans,* pp. 93-94.

# GENETICS OF THE BURMESE CAT

JOSEPH C. THOMPSON, VIRGINIA C. COBB, CLYDE E. KEELER*, AND MADELEINE DMYTRYK

THE first "Burmese" cat (see Figure 10) was a female imported into the United States from Burma by the senior author in the year 1930. Its bodily confirmation and behavior were typical for native Malay cat stocks, best represented in America by the Siamese variety. The Burmese was not recognized at once by the fanciers as a new breed, but suffered for some time the onus of being considered by most persons as an "off-colored Siamese." This explanation sounded very plausible to owners of Siamese who knew that usually the body color of the Siamese darkens with age and varies to a certain extent with the seasons of the year. To make matters worse, the first Burmese cat did not breed true, but threw both Burmese and Siamese kittens when mated to its nearest available Malay cat type, the Siamese (see Figure 13*D*).

Two of the present authors (C. E. K. and V. C.C.) at once recognized the first Burmese cat as belonging to a new "incipient true-breeding variety." On the basis of crosses made by the senior author, and through a paper (by C. E. K. and V. C. C.) in 1934 one of us (V. C. C.) proposed[1] to the Cat Fanciers Association that the Burmese be recognized as a new color variety for show purposes. Agitation was continued until its acceptance in 1936. Burmese are now eligible for registration in the Association Stud Book.

Further crosses by the senior author produced the foundation pedigree of the breed, shown in Figure 11. In this chart it will be noted that, starting with the imported Burmese cat, Wong Mau, containing one gene for Burmese and one gene for Siamese, and by mating this to a Siamese, Tai, it has been possible to establish a Burmese variety that has bred true for three generations.

The official standards[2] for Burmese call for a Siamese conformation, a chocolate brown body color with seal points, and topaz eyes. The kinky tail common to so many Malay cats has not been bred out of Burmese stock and is generally present.

It was recognized that Mendelian segregation of two coat colors was taking place in crosses of the imported Burmese to a Siamese male, as will be seen in Figure 13*D*. The light colored kittens always developed into typical sealpoint Siamese cats with china blue eyes, and the dark kittens all became Burmese cats with topaz colored eyes. There were no intermediate color gradations observed.

From crosses of this sort made by the senior author there resulted 11 Burmese males, 16 Burmese females, 11 Siamese males and 10 Siamese females.

Mr. Mel Friedlander mated a Burmese female with a Siamese male. This cross produced four Siamese and four Burmese.

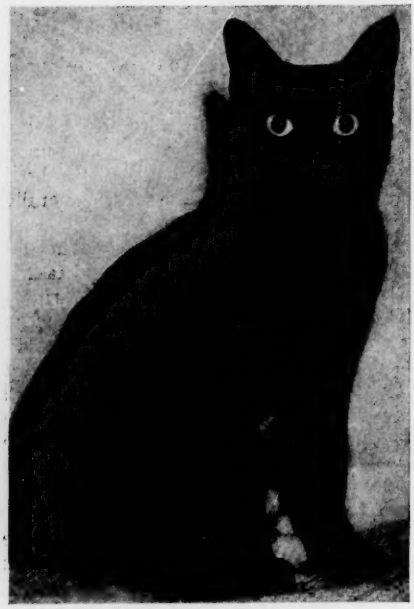
One of us (V.C.C.) crossed a Burmese female to a Siamese male. There resulted three Siamese and two Burmese. In all, such crosses have produced a total of 34 Burmese : 27 Siamese.

Because these four segregating classes were present in relatively equal numbers, it was suspected that they represented a monofactorial backcross involving one contrasted pair of autosomally borne gene alleles, or that some independent autosomal gene manifest only in the presence of the Siamese pattern, was converting certain genotypically Siamese kittens into Burmese.

It soon became apparent that all genes involved must be autosomal because of the numerical equality of the sexes in both Siamese and Burmese catagories. Thus, the possibility of the genetic complication of sex-linkage was readily dismissed.

It had been shown previously by two of the authors (C.E.K. and V.C.C.) that

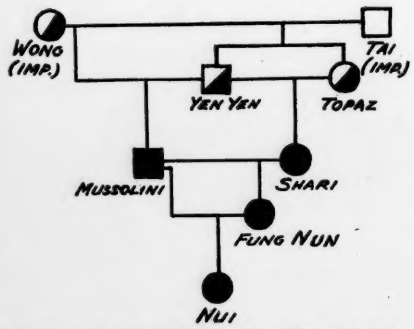
*The Edgewood School, Greenwich, Connecticut.



**TOPAZ MAU, BURMESE**

**Figure 10**

Daughter of the first Burmese cat, Topaz Mau illustrates the type. Burmese is a dark variant of the Siamese. It is an intermediate allelomorph of the albino series, between silver and Siamese.




**FOUNDATION STOCK OF THE BURMESE VARIETY OF CATS**

**Figure 11**

Squares represent males, and circles females. The solid black symbols indicate pure breeding Burmese. The half shaded symbols indicate Burmese × Siamese hybrids which carry one gene for Burmese and are intermediate in color. The unshaded symbols indicate the pure Siamese. The production of a pure breeding Burmese breed was very easy because of the intermediate coloring of the Burmese × Siamese hybrids. (See Figure 12.)

the gene producing "Silver" or "smoke" (Figure 13*C*) in cats is an allele or alternative form of the same gene that produces the Siamese coat pattern. Both silver and Siamese coats are affected by temperature and age, and both types have points darker than the body color. This is more evident in the non-agouti or non-tabby form, namely, smoke.

From the results of these experiments, coupled with the fact that the Burmese also has dark points and that the body coat darkens with age, it appeared that Burmese might well represent a physiological intermediate between silver and Siamese. If a physiologically intermediate stage between these two coat colors, it appeared probable that it might be an allele. The breeding experiments were henceforth conducted to test this hypothesis.

If Burmese represents an intermediate allele between silver and Siamese, we can make the following predictions:

1. When Burmese is crossed to normal intensity (Figure 13*B*) all of the offspring will exhibit normal intensity of pigmentation.

2. When pure bred Burmese is mated to Siamese, all the kittens should be Burmese.

3. All Siamese segregates from crosses involving Burmese should breed true for Siamese.

4. When Burmese (whether pure-bred, or hybrid for Siamese) is mated to silver or smoke, the offspring should all be silver or smoke rather than tabby or black, as is the case when animals bearing two Mendelian coat colors due to genes at independent loci are involved.

The stud, Pak Kwai Mau (Siamese segregate of the first Burmese, Wong Mau by a Siamese sire, Tai Mau) has sired more than 500 kittens of Siamese queens. All of these kittens have been Siamese without a suggestion of Burmese. Nor have the authors ever heard of Siamese cats having Burmese ancestry, throwing Burmese unless mated

**COLOR VARIATION IN KITTENS**

**Figure 12**

These three grades of pigmentation of the Siamese and Burmese coats are shown in the kittens. Left to right: thoroughbred Siamese, hybrid Burmese × Siamese, and purebred Burmese. The heterozygote carrying both the Burmese and Siamese alleles is intermediate in color.

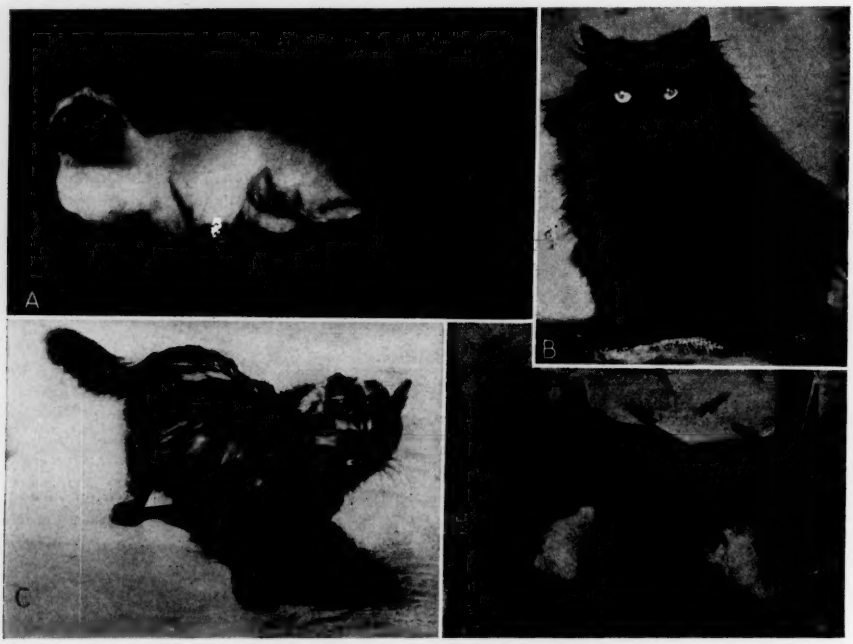
with Burmese. These facts are in line with prediction No. 3.

Burmese has been outcrossed to cats of normal coat color intensity. All the kittens so produced were of normal intensity. This confirms prediction No. 1.

It was learned that where there was opportunity for the Burmese gene to enter a cross from both parents, there might be in addition to Siamese kittens, two shades of Burmese kittens (Figure 12). The lighter of the two shades developed into the coat color of Wong Mau. The darker shade developed into a darker body color.

It is well known that in rabbits, rats and mice an animal showing a member of the albino series of allelic coat colors will be lighter when hybrid for a lower allele than if purebred for the given first allele. Aware that we were probably dealing with alleles of the albino series in the cat, we suspected that these two types of Burmese represented animals purebred for the Burmese gene (darker) and hybrid for the Siamese gene (lighter), respectively. A cross of dark Burmese to Siamese yielded only Burmese kittens, in keeping with prediction No. 2.

Where two Burmese, each hybrid for Siamese, were mated, the 3:1 ratio was observed. The verification matings by one of us (M.D.) gave 20 Burmese : 5 Siamese. When these 20 Burmese were divided as to color phase there were found 3 dark and 17 light. We actually




**ALLELES OF THE ALBINO SERIES**

**Figure 13**

At the present time four alleles of albinism are known. These are shown here. The lightest form is the Siamese (*A*). Next in intensity of pigmentation is the Burmese (*D*), the kittens shown are segregating for Burmese and Siamese pigmentation. The smoke or silver pigmentation (*C*) is intermediate between Burmese and the full tabby or black pigmentation (*B*) shown here in a Persian kitten. A color intermediate between Burmese and Siamese has also been reported, and complete pink-eyed albinism would also be expected to be a member of this series.

expect twice as many light as dark for a Mendelian explanation.

Prediction No. 4 was the most difficult of all to test, because so many matings between Burmese and Smoke failed to produce offspring, to such an extent that it was suspected that some sort of physiological block prevented interfertility between these two varieties. But the persistence of one of us (M.D.) eventually resulted in a fruitful mating. A Smoke-Persian female (see Figure 13*C*) was mated to a Burmese (hybrid for Siamese). Five kittens resulted, all smokes. This confirmed our final prediction, No. 4.

## Conclusion

Thus, we may conclude from the results of all our genetic tests that:

1. The Burmese is a distinct, new coat-color variety of the domestic cat, having a sound genetic basis, in that dark Burmese will breed true.

2. The Burmese coat color is based upon the possession of a pair of Burmese genes (dark color phase) or of a single Burmese gene and its Siamese gene allele (light phase).

3. Burmese and Siamese genes are sharply contrasted in their effects, there being no intermediate grades of coat color observed, and Mendelian ratios being found in both $F_2$ and backcross matings.

4. The Burmese gene represents a fourth identified allele in the albino series which, naming the genes in order of diminishing pigmentation produced, are as follows:

1—Normal intensity (Tabby or Black)

2—Silver (Smoke)
3—Burmese
4—Siamese

### Postscript

A color variation darker than ordinary Siamese was discovered by Lelia Volk of Honolulu to be segregating in her Siamese strain. This was examined by one of us (C.E.K.) and found to be intermediate in color between Burmese and Siamese, and hence we suspect the Hawaiian variation to represent a fifth allele in the albino series. It is so near Siamese in color, however, that it will probably not be perpetuated as a distinct variety and hence the possibility will probably not be had of checking its genetic relationships. At least one intermediate allele between the one producing an intensity similar to that of Burmese and the one producing Himalayan is known in rabbits, and a similar gene[4] (extreme dilute of Detlefsen) is known in mice. These facts seem to make our suspicion of the Honolulu variation representing a fifth albino series allele in cats seem even more plausible.

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## ARE WAR MARRIAGES EUGENIC?

SOME notes based on discussions with college students. The discussions were centered on the hasty marriages of young men who are going away in the armed services.

*A*—It seems probable that from the eugenic point of view the war marriages are far more satisfactory than average marriages of young people of the same ages. Whether they are socially desirable is another matter to be considered later.

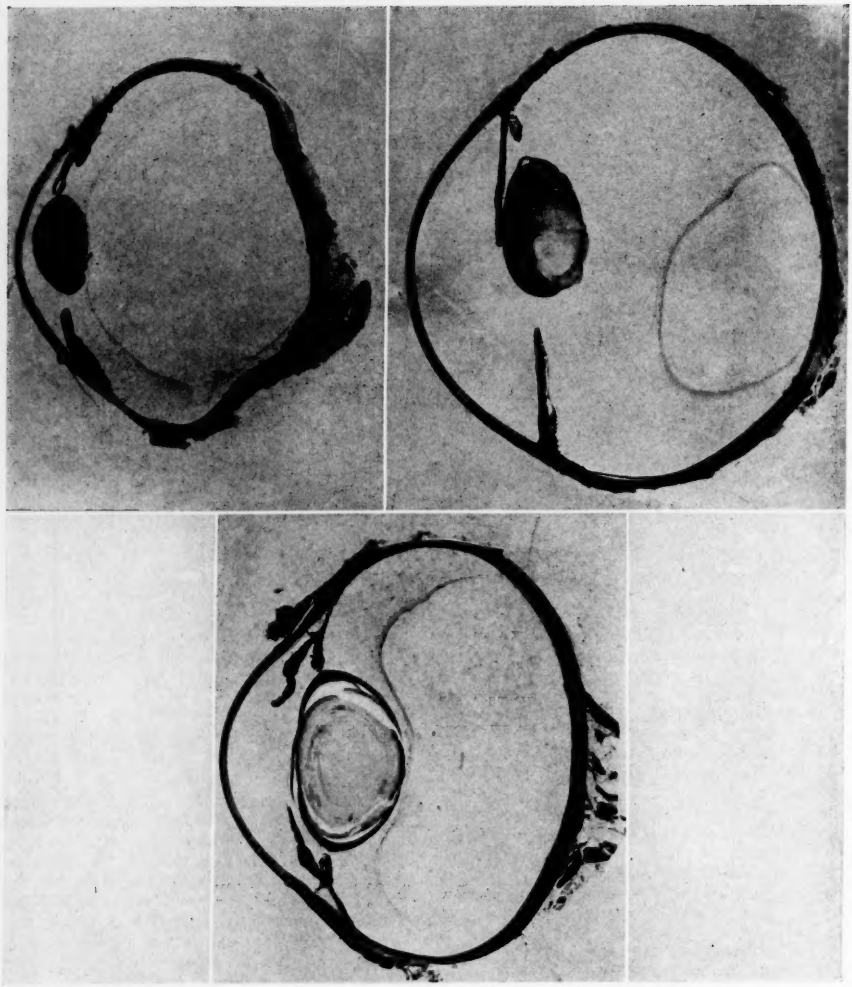
War marriages tend to be eugenic because (1) The young men going into the armed services are selected on the basis of physical and mental tests. While these tests apply only to the individual and do not consider genetics, they certainly in the mass tend to select extra good genetic probabilities. (2) The selected men of the armed service tend to marry women whose physical and mental qualities appear to be very good. We could be more certain on this point if many thousand recent war brides were given the physical and mental tests required of their husbands. Guessing is not science, but it is a safe guess that the vast majority of the war brides would pass the tests that selected their husbands for service. In this connection it is interesting to mention that there are some good reasons for expecting that a smaller percentage of women than of men would have been rejected if the two sexes had been called on the same basis to the selective examinations. (We must keep in mind in these discussions that many defects which affect health and efficiency in the armed services have nothing to do with heredity and eugenics.)

Summary: From the eugenic point of view war marriages look promising. They are as eugenically good as we could make them if the army medical and mental tests were required for all marriage licenses. We could do better only by requiring genetic examinations for licenses. After the war we are going to be much more interested in physical and mental examinations as a basis for proposed health improvement campaigns. Perhaps indirectly this will encourage interest in the eugenic movement.

*B*—The students in these discussions were more interested in the social aspects of war marriages. It was agreed that from the social point of view the hastily planned marriages (not the long engagements) were problems. That proved so in many such marriages in 1917-19. Hasty war marriages are probably greater risks than hasty marriages in normal times. The reason may be that in wartime the wedding is commonly followed by long separation without the opportunity for post-nuptial adjustments that so often make hasty marriages successful when the newly-weds live and work and play together after the wedding.

Summary: In the cases of preceding close acquaintance, especially engagements, immediate marriages when the men were leaving for war in 1917-19 were commonly socially successful. Hasty marriages based on short acquaintance and wartime emotions were so often social failures that they should not be recommended under present conditions. Most participants in the discussions were inclined to admit that it is now impossible to plan post-war economic matters affecting families from war marriages or any others. Hence economic arguments have little weight with the young folks concerned.

M. A. BIGELOW.



**SECTIONS OF NORMAL AND CATARACTOUS EYES**

**Figure 14**

Saggital sections taken through the greatest diameter of the eyes of two cataractous cows (above) compared with the eye of a normal cow two years old (below). Cataractous eye at the upper left is from male calf 735B two and half months of age. The lens is abnormally placed and reduced in size. Note the large degenerating nucleus and the thin peripheral border of normal appearing fibers. The degenerative changes taking place have not yet reached the more advanced stage observed in the older animal. The other cataractous eye is that of cow 581, eight years of age. The lens is small and misplaced. Note the increased depth of the anterior chamber angle. Progressive degeneration has destroyed the crystalline appearance of the lens. Some of the changes may be attributed to incrased intra-ocular tension that caused the eyeball to expand and the cornea to protrude or bulge forward.

# A CONGENITAL HEREDITARY EYE DEFECT OF CATTLE

P. W. Gregory, S. W. Mead and W. M. Regan
*Division of Animal Husbandry, University of California*

OUR inbreeding experiments with Jerseys, designed to fix the factors for high milk and butterfat production into a more homozygous state, have brought to light several undesirable recessive genes. The first to be reported[4] was a congenital epithelial defect lethal in nature and commonly known as "hairless." The second, a recessive type of achondroplasia, is also lethal and is apparently different from any other yet reported in cattle.[2] A third character segregated from the stock is a type of proportionate dwarfism, apparently conditioned by a single autosomal recessive gene.[3]

A fourth anomaly has now been uncovered. It is congenital and affects the eyes, impairing the vision. There is considerable variation in the phenotypic expression of this mutant type. At birth the eyes may be normal in size or somewhat reduced. The most reliable diagnostic character is the appearance of the lens, which shows as an opaque body beneath the cornea. As an animal becomes older there are progressive changes in the affected eyes, although here again there is considerable variation. Often the cornea becomes enlarged and distorated in shape as if under hydrostatic pressure. When a defective animal stands facing the sun, there is a tendency to keep the eyes partially closed as if sensitive to strong light. There is apparently a considerable reduction in vision, although total blindness is unlikely except perhaps in extreme cases.

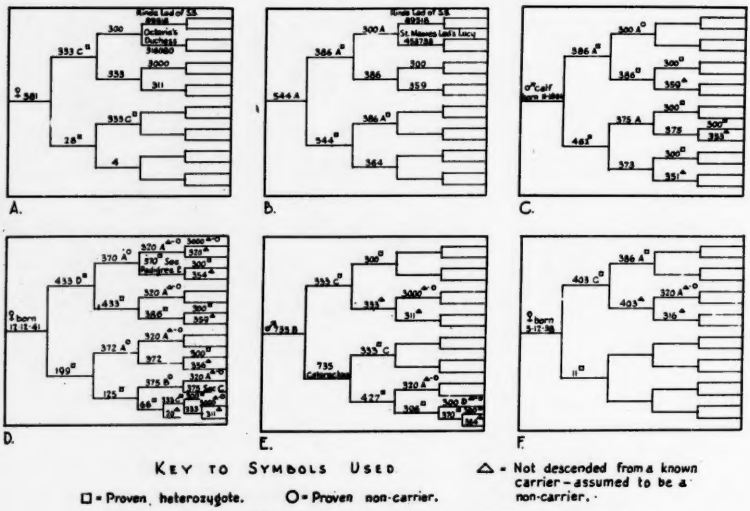
The animals used in this study include not only those of the University herd, but cattle in the herds of cooperating dairymen who were using University sires. Having principally grade cows, these dairymen do not sell bulls for breeding, hence most of the males are destroyed at birth. Since the opaque lens may be easily recognized even in young calves, it is improbable that any defective animals were overlooked after the defect was discovered.

### Genetic Analysis

The records of all calves with defective eyes are assembled in Table I. A total of 16 were produced, ten in the University herd and six in the herds of three cooperating dairymen *A*, *F*, and *D*, who were using University sires. The first defective animals were found in herd *A;* male No. 1 and female 581. Both resulted from mating bull 333*C* to his own daughters (Table I and pedigree *A* (Figure 15).

At the time bull 333*C* was producing calves with defective eyes in the herds of cooperating dairymen, bull 386*A* sired two calves with defective eyes in the University herd (Table I and pedigrees *B* and *C*). Since sire 333*C* produced more defective-eyed progeny than all the other sires combined (11 out of a total of 16), his matings will be used to determine the inheritance of the defect. Table II summarizes the results of two types of matings. In the first, 333*C* was bred to his own daughters (pedigree *A*) and produced a total of 27 progeny. In the second (pedigree *E*) he was mated to defective-eyed cows and produced nine progeny. It will be observed (Table II) that the expected results on an autosomal monofactorial recessive basis are approached very closely and are in general agreement for both types of matings even though no defective females were produced in the second group.

When all the other matings are taken into account, an autosomal monohybrid recessive interpretation is consistent with the observed results. All heterozygous animals have normal eyes.




**PEDIGREES OF CERTAIN CATARACTOUS CALVES**

**Figure 15**

By cross-checking such a group of interrelated pedigrees it is frequently possible to determine which of the potential carriers actually transmit a given defect.

## Origin of the Mutant Gene

Since 333*C* and 386*A* were related and both sired calves with the eye defect it is logical to suspect that each obtained the mutant gene from the same source. This was definitely determined through progeny tests and pedigree studies. In pedigree *A* it will be seen that 333*C* is the sire and grandsire of defective cow 581. Hence 333*C* is a proved heterozygote and this suggests that either sire 300 or sire 3000 may have been the carrier that introduced the gene into the University herd.

As shown in pedigree *B*, bull 386*A* and cow 544 are proved heterozygotes since they produced the defective-eyed male 544*A*. Sires 386*A*, 333*C*, and cow 544 evidently obtained the gene from a common ancestor. Pedigree *B* acquits sire 3000, but suggests that sire 300*A* as well as 300 may have been a carrier. Since sires 300*A* and 300 are paternal half brothers, both could have been carriers if their sire were heterozygous. Pedigree *C* proves that sire 300 is heterozygous but does not absolve sire 300*A*. By checking the results obtained from mating 300*A* to daughters of 300 and from mating heterozygous sire 386*A* to daughters of 300*A*, it was possible to determine that 300*A* was a noncarrier. Sire 386*A* therefore obtained the gene from 300 through cow 386.

Pedigrees *D* and *E* are interesting because progeny tests have been employed to determine the genotypes of all the sires that appear in both pedigrees. With this information at hand, one can trace the mutant gene through normal carrier cows that could not be proved otherwise. In pedigree *D*, sires 370*A*, 320*A*, and 3000 are demonstrated to be homozygous normal. Evidently, then, 433*D* obtained the defective gene from sire 300 through cows 386 and 433. Bulls 372*A* and 375*B* are proved noncarriers. It is therefore obvious that cow 199 obtained the mutant gene from 300 through 333*C* and cows 66 and 125. Pedigree *E* proves cows 427, 396, and 370 to be heterozygous.

Sire 573*A* had normal eyes, but produced a defective-eyed calf in cooperating herd *D* when bred to normal cow 215 (Table I). Sire 573*A* obtained the

mutant gene from 333*C*; his sire, grandsire, and great grandsire. Cow 215 obtained the gene from 300 through either her sire or her dam, since both are descendants of 300.

With but two exceptions both the sire and the dam of each calf born with defective eyes were descended from sire 300. As Table I shows, cow 11, a registered Jersey and foundation cow in herd *F*, produced two calves with defective eyes. This cow did not descend from 300 or from any proved carrier. The sire of the first calf was 333*C*. Cow 11 is therefore heterozygous for the defect. The second defective-eyed calf produced by cow 11 was sired by 403*C* (pedigree *F*). This bull obtained the mutant gene from sire 300, but it is impossible to determine how cow 11 obtained the gene. Heterozygous sire 300, Octavia's Rinda Lad, registry number 188257, and cow 11 when traced back five generations, descended from many common ancestors. Cow 11 and sire 300 probably obtained the mutant gene from the same source.

## Economic Importance

All defective-eyed cows showed normal reproduction. Although they appear to possess the qualifications necessary for high milk production, they produced less milk and fat than their normal sibs. This may be attributed to an inability to compete successfully with the normal cows in the feeding corral and to a marked excitability in the milking barn. All the defective-eyed cows were rather apprehensive in close quarters, probably because of their poor vision. Since the care which would be required in the handling of these cows for maximum production would be impractical this defect has considerable economic importance.

## Gross Appearance of the Living Cataractous Eye

An ophthalmologic study was made of two defective animals, one a year of age and the other five. In the former the lens was dislocated temporally and slightly upward so that the lens occupied only the temporal two-thirds of the pupilliary area. It appeared to be somewhat smaller than the normal. Some of the fibers in the suspensory ligament could be seen stretching across the por-

**TABLE II. Results of mating 333C to his own normal-eyed daughters in the U. C. herd.**

| | Normal eyes | | Defective eyes | |
|---|---|---|---|---|
| | Male | Female | Male | Female |
| Observed | 11 | 12 | 2 | 2 |
| Expected | 11.8 | 11.8 | 1.7 | 1.7 |
| d | − .8 | + .2 | + .3 | + .3 |

**Results of mating 333C to defective-eyed cows in the U. C. herd.**

| | Normal eyes | | Defective eyes | |
|---|---|---|---|---|
| | Male | Female | Male | Female |
| Observed | 3 | 3 | 3 | 0 |
| Expected | 2.25 | 2.25 | 2.25 | 2.25 |
| d | + .75 | + .75 | + .75 | −2.25 |

**TABLE I. Tabulation of all calves born with defective eyes.**

| Number | Sex | Date born | Sire | Dam | Dam's sire | Herd |
|---|---|---|---|---|---|---|
| 1 | Male | 1/30/33 | 333*C* | 28 | 333*C* | *A* |
| 581 | Female | 2/12/33 | 333*C* | 30 | 333*C* | *A* |
| 2 | Male | 11/10/34 | 386*A* | 462 | 375*A* | U. C. |
| 3 | Female | 1/30/35 | 333*C* | 11 | ---- | *F* |
| 544*A* | Male | 9/15/35 | 386*A* | 544 | 386*A* | U. C. |
| 702 | Female | 3/5/36 | 333*C* | 572 | 333*C* | U. C. |
| 735 | Female | 8/31/37 | 333*C* | 427 | 320*A** | U. C. |
| 4 | Female | 5/12/38 | 403*C* | 11 | ---- | *F* |
| 5 | Male | 6/14/39 | 333*C* | 702 | 333*C* | U. C. |
| 572*C* | Male | 3/5/40 | 333*C* | 572 | 333*C* | U. C. |
| 6 | Male | 3/10/40 | 333*C* | 581 | 333*C* | U. C. |
| 7 | Male | 6/3/40 | 333*C* | 711 | 333*C* | U. C. |
| 807 | Female | 5/18/40 | 333*C* | 572 | 333*C* | U. C. |
| 8 | Male | 8/2/41 | 573*A* | 215 | 371*C* | *D* |
| 735*B* | Male | 8/10/41 | 333*C* | 735 | 333*C* | U. C. |
| 9 | Female | 12/12/41 | 433*D* | 199 | 372*A** | *A* |

*Proved noncarrier.

tion of the pupil not occupied by the lens. The equatorial rim of the lens where seen in the pupilliary area was slightly irregular. The immediate sub-capsular stratum of the lens was clear, but a broken opaque plaque was present in the perinuclear region of both the anterior and posterior cortex. The nucleus, as far as could be determined, contained no opaque bodies.

In the adult cow the lens was dislocated temporally and upward so that it occupied only the temporal one-half of the pupillary area. This lens was definitely reduced in size. The equator of the lens as seen in the pupillary area was fairly well delineated, having very little irregularity. Some of the fibers of the suspensory ligament could be seen stretching across the lenseless nasal half of the pupillary area. The lens cortex was densely opaque throughout and light was transmitted only to a depth just beneath the lenticular capsule. Ophthalmoscopic examination through the clear nasal portion of the pupil showed fairly normal retinal structure as compared to the normal cow's eye. The prepared sections corroborated these observations. (Figure 14.)

Detlefson and Yapp[1] reported in Holsteins a congenital eye defect conditioned by a recessive gene. Small,[5] using an ophthalmoscope to study the eyes of these animals, identified the anomaly as a type of cataract. His description agrees with our observations rather well.

The cataractous eyes of two of our animals were sectioned for histological examination. Cow 581, an eight-year old, manifested the defect to an extreme degree. Her eyes were enlarged and misshapen, with a pronounced bulging of each cornea. Calf *735B* was less than three months of age. His eyes appeared typical of defective specimens for that age. The lenses were opaque but otherwise the eyes appeared normal. An eye from a normal animal, about two years of age, was also sectioned for comparison. The same technique of fixing, staining, and sectioning was employed for all the eyes. Photographs of sagittal sections through the greatest diameter are shown and described in Figure 14. Attention is directed only to the more obvious modifications. A detailed study might reveal other pathological conditions, more interesting to the ophthalmologist.

When the cataractous Jerseys are compared with the cataractous Holsteins, there are many characteristics common to both. Small's[5] description of the cataractous eyes of Holsteins applies equally well to our Jerseys. He found that the lenses of cataractous animals are reduced in size and that young animals do not have the advanced degenerative changes found in older animals with mature cataract. We conclude, therefore, that the cataractous condition of Jerseys is probably identical with that of the Holsteins studied by Detlefson and Yapp[1] and by Small.[5]

The authors are indebted to Mr. A. C. Anderson, a graduate student in the Division of Animal Husbandry of the University of California, for preparing the sections used in this study, and to John E. Gray, M.D., for advice and assistance in studying these sections and also the defective eyes in vivo.

## Summary

A congenital type of cataract has been found in the purebred Jersey herd of the University of California. In both young and adult animals the lens is dislocated and smaller than normal. In calves the cataract is of the perinuclear type, while in the adult the cataract has progressed to the mature stage. This anomaly is hereditary and conditioned by a single autosomal recessive gene. It appears to be identical with the congenital hereditary cataractous condition reported in Holsteins from the Illinois Experiment Station.

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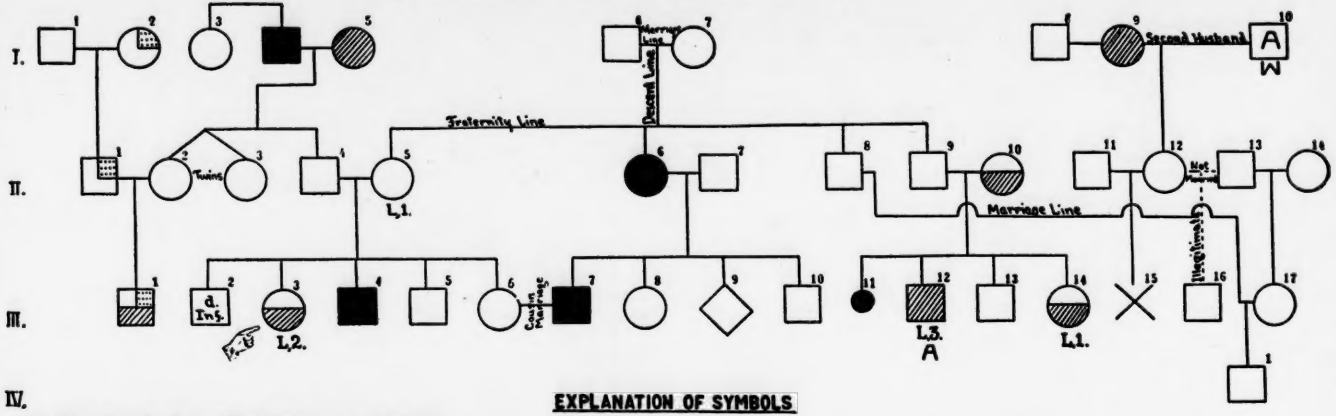
# SAMPLE PEDIGREE CHART SHOWING THE MANNER OF CONSTRUCTION, AND THE USE OF STANDARD AND SPECIAL SYMBOLS.




## EXPLANATION OF SYMBOLS

**(a). Standard for all Pedigree Charts:**

□=Male; ○=Female; ◇=Sex unknown; ●=Still-birth or Miscarriage; X=Children — number and sex unknown; ○○=Twins; d.Inf.=Died in Infancy; ☞ Points to the Propositus or central figure in the pedigree.

□—○=Parents.

□○□○○=Children.

Roman figures to the left indicate generations; Arabic figures locate individuals, (thus III.7 is the young man in the third generation who married his cousin).

The following letters, placed in or around the individual's pedigree symbol, are standard for certain traits: A, alcoholic; B, blind; D, deaf; E, epileptic, F, feebleminded, I, insane, M, migraineous; N, normal in reference to traits under consideration; Ne, neurotic; P, paralytic; Sx, sexually immoral; S, syphilitic; T, tuberculous; W, wanderer.

**(b). Especially devised or selected for this particular pedigree-chart:**

■●=Successful leaders in politics. ◪◔=Extra thumb on right hand. L.1.=Highly successful author. L.3.=Little or no ability in literary efforts. ▨◍=Superior in vocal music. ▨◍=Medium attainment in vocal music.

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Prepared by the International Commission of Eugenics. See *Journal of Heredity* for August 1926. Additional copies may be obtained from A.G.A.